CHROMOSOME NUMBERS IN THE HAMAMELIDACEAE AND THEIR PHYLOGENETIC SIGNIFICANCE

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With three text figures

Reinsch[1] introduced his morphological survey of the Hamamelidaceae by the observation that they form one of those natural families as to whose precise delimitation and relationships there has been much difference of opinion. The forty years which have elapsed since the appearance of his paper have merely provided further illustrations of the justice of his remarks. Though universally conceded to be a natural group, the only general agreement as to its phylogenetic position seems to be the opinion that it occupies an important one. Because of this uniformly recognized phylogenetic significance an effort has been made to make as complete a survey of chromosome numbers as possible. The living collections of the Arnold Arboretum fortunately include several genera such as *Sinowilsonia* and *Parrotiopsis* which are very rare in cultivation but the work has been hindered by the very great technical difficulties involved. The chromosomes are small, there is much secondary pairing, the cytoplasm is murky and the chromosomes do not stain sharply. In most of these details the family shows cytologically a strong resemblance to the Rosaceae, paralleling the morphological resemblances which have been commented on by most students of the group.

The following chromosome counts have been made. The genera are arranged according to the classification of Harms in Engler and Prantl. In each case the counts were obtained from aceto-carmine smears. Typical meiotic plates are illustrated in Figure 1.

Sub-family Hamamelidoideae		Chromosome Number
Tribe 1	Hamamelis vernalis	12
Tribe 3	Corylopsis pauciflora	12
	Corylopsis spicata	36
	Corylopsis Veitchiana	36
Tribe 4	Parrotiopsis Jacquemontiana	12
	Fothergilla major	36
	Fothergilla monticola	24
Tribe 5	Sinowilsonia Henryi	12
Sub-family Liquidambaroideae		
	Liquidambar Styraciflua	15

[1]Engler in Bot. Jahrb. **11**: 347 (1890).

Meiotic irregularities, accompanied by a high percentage of pollen sterility were encountered in *Liquidambar Styraciflua*. This is somewhat puzzling since this species exhibits none of the morphological peculiarities which are usually associated with irregular meioses. It is a "good" species with no closely related forms occurring within the same area. Its behavior is more probably to be explained as due to climatic influences. It is a southern species and at the Arboretum is being culti-

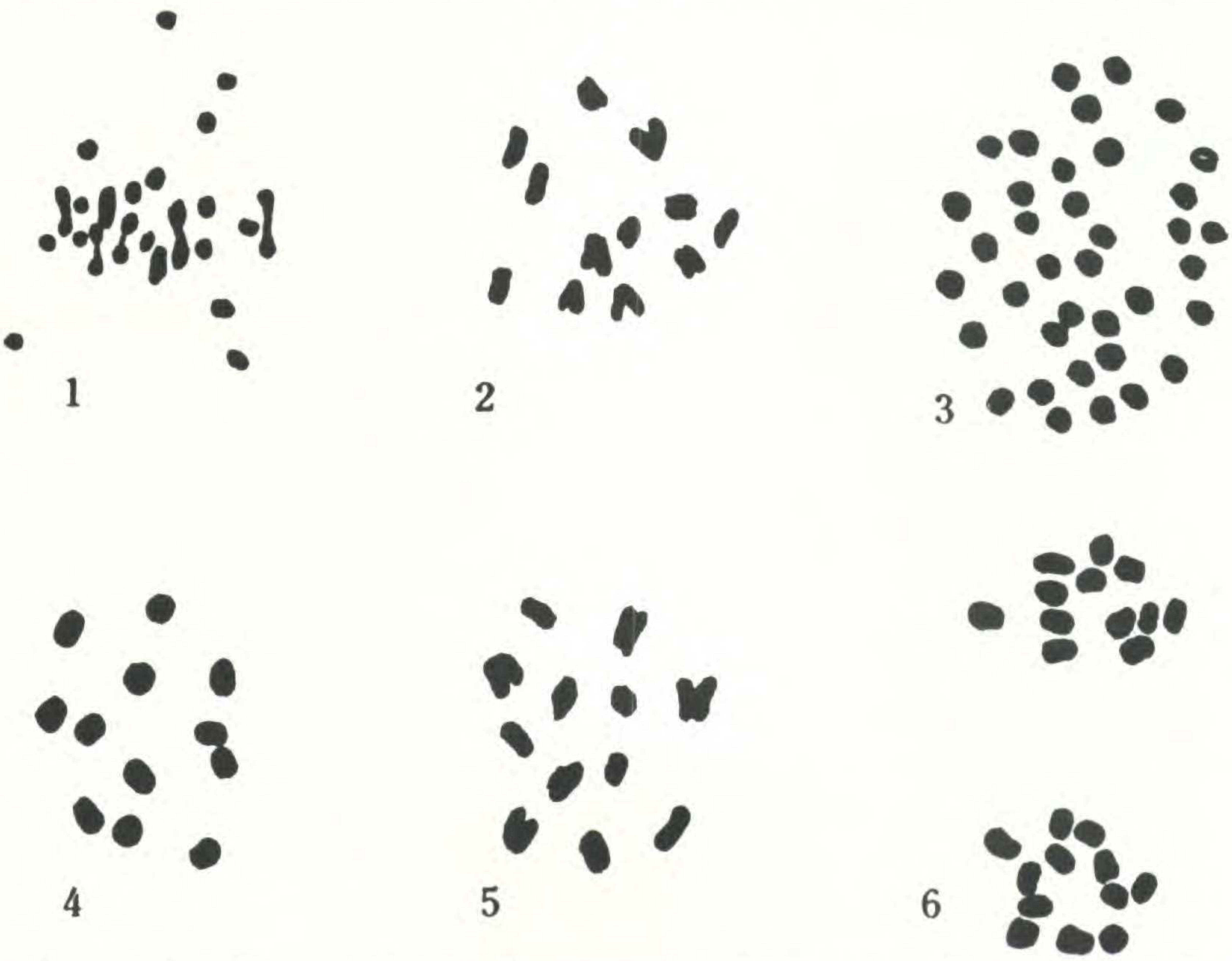

FIGURE 1. Camera lucida drawings (× 3000) of pollen mother cells: 1. Liquidambar Styraciflua. — 2. Parrotiopsis Jacquemontiana. — 3. Fothergilla major. — 4. Corylopsis pauciflora. — 5. Sinowilsonia Henryi. — 6. Hamamelis vernalis.

vated somewhat north of its natural range. Whitaker[1] has demonstrated the effect of abnormal temperatures upon meiosis in *Cyphomandra*. It is possible that the irregular chromosome behavior and consequent pollen sterility of *Liquidambar Styraciflua* at the Arnold Arboretum may have a similar explanation. It would be interesting to know if *L. Styraciflua* is characterized by low percentages of fertile pollen in its native home.

The cytological studies present a number of facts of taxonomic significance. 1. The Hamamelidoideae are a coherent group with a com-

[1]Jour. Arnold Arb. **15**: 113–117 (1933).

mon base number. 2. The count on *Liquidambar* suggests that the Liquidambaroideae may possibly be derived from a different stock than the Hamamelidoideae since they apparently have a different base chromosome number. If this difference in base number should be found to persist in the other genus of that sub-family it would indicate that the divergence between the two sub-families occurred before the differentiation of the family as a whole. This is in accordance with the views expressed by Harms.[1] Summarizing the anatomical evidence he states[2] that the Hamamelidoideae are a unified group anatomically while the other subfamilies, particularly the Liquidambaroideae, have many distinctive peculiarities. Reviewing the entire evidence of relationship[3] he suggests that the Liquidambaroideae are so distinctive that they might well be considered a separate family.

3. Polyploid series have been found in *Fothergilla* and *Corylopsis* and are not to be unexpected in other genera of the family when these are investigated more extensively. This discovery is of some taxonomic consequence since it indicates that in such genera we may expect phylogenetic relationships between species which will be, in part at least, reticulate. That is to say that a complete phylogenetic tree of the genus *Fothergilla* or *Corylopsis* would show anastamosing branches. It will be noted that *Fothergilla monticola* has 24 pairs of chromosomes and is therefore a tetraploid and that *F. major* with 36 pairs is a hexaploid. The phylogenetic relationships within and between these two species, as indicated by these chromosome counts, must be intricate. These two species are so similar that it is very doubtful if *F. monticola* deserves more than varietal rank.[4] The cytological evidence would suggest that *F. monticola* is merely a tetraploid variety which arose spontaneously from the hexaploid species *F. major*. Such relationships are not unknown in other genera of the flowering plants. Erlanson for instance has shown[5] that *Rosa acicularis* var. *Sayi* (Schw.) Rehder is an octoploid race ($2n = 56$) of the hexaploid species *Rosa acicularis* ($2n = 42$).

To the larger problem of the phylogenetic position of the family itself this cytological survey contributes important evidence, though unfortunately not as decisive as the obscurity of the case requires. Before going into details it may be said that on the whole the cytological evidence favors Hutchinson's interpretation of the phylogenetic position of

[1] Engler Prantl Nat. Pflanzenf. 2. Aufl. **18a**: 303–345 (1930).
[2] loc. cit. p. 307.
[3] loc. cit. p. 316.
[4] Anderson in Arnold Arb. Bull. Pop. Inform. ser. IV, **1**: 61–64 (1933).
[5] Bot. Gaz. **96**: p. 231 (1935).

the Hamamelidaceae.[1] Comparisons of two treatments of the family are presented in Figure 2. The numbers in the diagram are the base chromosome numbers so far as they have been determined.[2, 3]

By inference and by actual experimental test two kinds of change of chromosome number have been established as occurring in the higher plants; (1) the addition of whole sets of chromosomes, that is of two

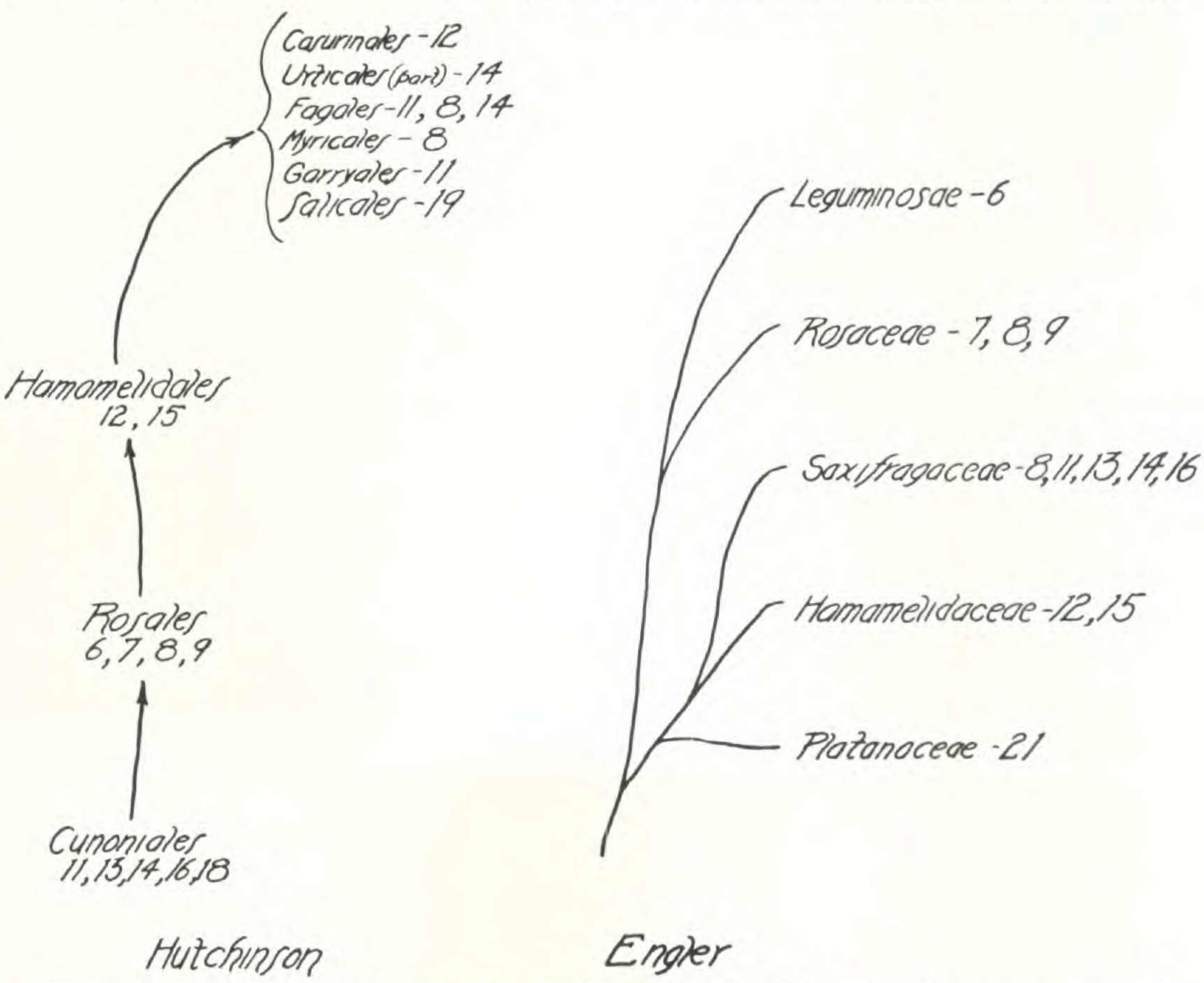

FIGURE 2. The phylogenetic position of the Hamamelidaceae, according to Hutchinson and Engler. The numbers are the basic chromosome numbers, so far as is known.

sets of six to make a 12 or the addition of an eight and a nine to make a 17; (2) the gradual stepping up or stepping down of the chromosome number by fusion and fraction of one or two pairs of the chromosomes in the previous set, that is, the derivation of an 11 chromosomed species from one with 12, etc. The whole subject is still in the experimental stage but it is at least far enough advanced to indicate that these two processes are among the main forces involved in the separation of genera in the higher plants. It will be seen that higher numbers may be derived

[1]The Families of Flowering Plants. I. Dicotyledons. Macmillan and Co., London 1926.

[2]Gaiser, L. O. in Genetic, **12**: 161–320 (1930).

[3]Sax, K. Published and unpublished work on chromosome numbers.

from lower by either process or by both, but that lower numbers can be derived from higher ones only by the second. Everything else being equal, therefore, those genera with high base numbers will be farther out towards the tips of the phylogenetic net-tree than those with much lower numbers. In the present case the cytological evidence favors the view that the Hamamelidaceae with their base numbers of 12 and 15 are derived *from* the Rosales stock where base numbers of 6, 7, and 8 are characteristic. Another cytological fact points in the same direction.

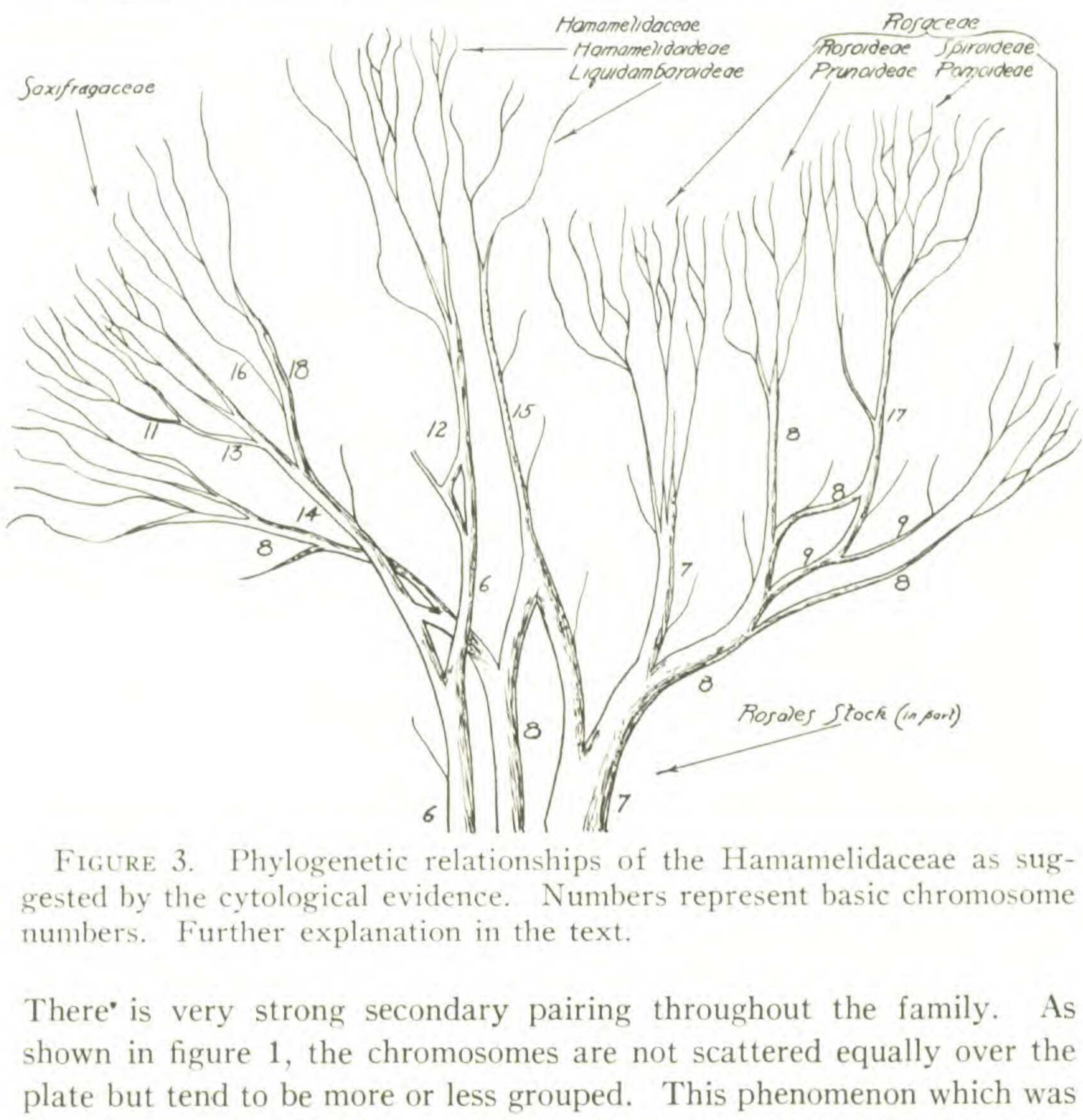

FIGURE 3. Phylogenetic relationships of the Hamamelidaceae as suggested by the cytological evidence. Numbers represent basic chromosome numbers. Further explanation in the text.

There is very strong secondary pairing throughout the family. As shown in figure 1, the chromosomes are not scattered equally over the plate but tend to be more or less grouped. This phenomenon which was first described by Darlington and Moffett[1] and which has been extensively studied by Lawrence[2] indicates that the chromosome complement under observation arose ultimately from the duplication of separate complements.

These facts, together with such other information as bears upon the subject, have been utilized in constructing the diagram in Figure 3. It

[1]Jour. Gen. 22: 129–151 (1930).
[2]Cytologia, 2: 352–384 (1931).

should be emphasized that the diagram is purely speculative. It has been worked out for those morphologists who would be interested in knowing how a cytologist with such information as is available would speculate as to the relationships of the groups involved. It might well be used as one of a set of possible working hypotheses by students of phylogeny. While the anastamoses of the main trunks of the Rosales stock represent supposed true-breeding allo-polyploid hybridizations, they do not necessarily indicate a cross between families as such. On any evolutionary hypothesis, related families derive, ultimately, from forms no more differentiated than present day genera or species. All that need be hypothecated for these hybrids is that they are between forms as diverse morphologically as certain hybrids which have been experimentally obtained, those between Zea and Tripsacum, for instance.[1] The diagram is based upon the evidence from chromosome number, secondary association and, in the case of the Pomoideae, from breeding experiments. It is much more speculative for the Saxifragaceae than for the Rosaceae. The Saxifragaceae, with base numbers of 8, 11, 13, 14, and 16 show a cytological complexity[2] paralleling their morphological diversity. Only a few of the fossil "dead branches" have been indicated. There must certainly have been many more. In this respect as in several others the actual details of the diagram are probably incorrect. The general conception, however, of a more or less webbed net-tree for the Rosales is strongly supported by the cytological evidence. In some other groups of the flowering plants (the Tubiflorae, for instance) the webbing would be so much more complex that one would scarcely use the word tree in describing it. In the Cyperaceae, on the other hand, there would be few if any anastamosing branches. The cyto-genetic evidence shows with increasing force that the actual pattern of evolutionary progress has been different in different groups of plants. The main point of the diagram in figure 3 is to suggest the general nature of the evolutionary pattern of the Rosales.

SUMMARY

1. Chromosome counts are given for nine species and six genera of the Hamamelidaceae.

2. The phylogenetic position of the family is discussed in the light of these results.

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[1]Mangelsdorf & Reeves in Jour. Hered. **22**: 329–343 (1931).
[2]Sax, K. in Jour. Arnold Arb. **12**: 198–206 (1931).